

Relationships of the Passerine Finches (Passeriformes: Passeridae)

by

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Introduction

The passerine finches are a small group of Old World seed-eating oscines consisting of the genera *Passer* Brisson 1760, *Montifringilla* Brehm 1828, and *Petronia* Kaup 1829. Their relationships to other groups of oscine finches have been a matter of disagreement for the past 75 years with no clear resolution. Discovery of a unique skeletal structure — the preglossale — in the tongue of the passerine finches (Bock and Morony, 1978) prompted us to inquire further into the taxonomic position of these birds. We would like to do so considering a series of hypotheses about groups and about characters (Bock, 1977: 875–891) pertaining to the passerine finches and to the preglossale and associated features. We accept, for this study, the approach and methods of evolutionary classification (see Bock, 1974, 1977). In this approach, the phylogeny and the classification of a group are not assumed to be redundant (i. e. redundant = the classification is an exact reflection of the phylogeny based upon the definition of relationship as being only that of phylogenetic branching), but that the classification reflects both the phylogeny and the amount of evolutionary

modification. Thus a clear distinction must be made between classificatory hypotheses about groups and phylogenetic hypotheses about groups. A further distinction must be made between these two types of hypotheses about groups and the diverse set of hypotheses about characters. Most important are the procedures used to test the hypotheses about characters against empirical observations — the character analysis phase of any taxonomic study. Once tested, the character hypotheses serve to test the various hypotheses about groups (see Bock, 1977, for a fuller discussion).

In addition to providing clues about the affinities of the passerine finches, the preglossale provides a good example to illustrate methods of phylogenetic analysis of taxonomic features. We would like to discuss the arguments and evidence used to test character hypotheses about the preglossale and associated features.

The hypotheses to be considered in this study are:

A) Classificatory hypotheses about groups:

1) That the passerine finches (i. e. the genera *Passer*, *Montifringilla* and *Petronia*) constitute a monophyletic taxon — the Passeridae or the Passerinae depending, in part, upon acceptance of one of the next three hypotheses — which includes no other genera of oscine birds.

2) That the passerine finches are members of the Fringillidae in the broad sense (we include only the finch-like birds, not all of the New World nine-primaried oscines).

3) That the passerine finches are members of the Ploceidae (either in the narrow sense or in the broad, i. e. containing the estrildids, sense).

4) That the passerine finches are a family-level taxon of oscines that have evolved features for seed-eating independently of the Fringillidae and the Ploceidae, and hence are not members of either of these groups. The closest relatives of the passerine finches must then be sought among all oscine birds, and the New World nine-primaried oscines cannot be eliminated from consideration.

B) Phylogenetic hypothesis about groups:

1) That the passerine finches had to evolve from an ancestral group possessing the M. hypoglossus anterior (a tongue muscle).

C) Hypotheses about characters:

1) That the preglossale is an homologous feature in the genera possessing it.

2) That the preglossale is an apomorph compared to the lack of this feature.

3) That the preglossale is a synapomorph (= homologous apomorph) in the genera possessing it.

4) That the presence of the M. hypoglossus anterior is plesiomorphous and its absence is apomorphous in the Passeriformes.

5) That the enlarged M. hypoglossus anterior with its sharply oblique fibers is homologous and apomorphous in the passerine finches compared to the usual structure (smaller with fibers arranged almost longitudinally) of this muscle in other passeriform birds.

Methods and materials

With few exceptions, all observations were made on fluid specimens preserved for gross anatomical dissection (preserved in 10 % formalin and stored in 60—70 % alcohol). Most specimens examined were in the collection of the American Museum of Natural History, a few were obtained especially for this study. A few skeletal specimens of passerine finches were examined when no fluid specimens were available. All dissections were made with the use of a Wild M5 dissecting microscope and all figures were drawn directly from the dissections with the use of a drawing tube (= camera lucida) attached to the microscope. The species examined are listed in the section on "Comparison."

Abbreviations

Bones

basihy = basihyale

ceratob = ceratobranchiale

parag = paraglossale

paragl = paraglossale

pre g = preglossale

Muscles

M b m = M. branchiomandibularis

M c g = M. ceratoglossus

t M c g = tendon of M. ceratoglossus

M c h = M. ceratohyoideus

M c r h = M. circohyoideus

M g g = M. genioglossus

M h g a = M. hypoglossus anterior

M h g o = M. hypoglossus obliquus

M m h = M. mylohyoideus

M s h = M. serpihyoideus

M s t h = M. stylohyoideus

M t r h = M. tracheohyoideus

M t r l = M. tracheolateralis

Other

d p = dermal papilla

g = gland

n = nerve

s c = sensory corpuscle

Taxonomic history of the passerine finches

During the last century and the early years of the present century, almost all workers regarded the passerine finches to be members of the fringillid finches (in the broad sense) and to be closest to the fringilline-cardueline group. Indeed the cardueline genus *Leucosticte* was included in *Montifringilla*. They were so treated by Sharpe in the "Catalogue of Birds in the British Museum" (vol. XII, 1888). Sharpe separated *Montifringilla* from *Petronia* and *Passer* by four genera. Further he included *Carpospiza brachydactyla* in *Petronia* (see below). Lafresnaye (1850) seems to be one of the very few early workers who disagreed with Sharpe's arrangement and suggested that *Passer* may be allied to the weaver-birds (Ploceidae) via the genus *Plocepasser* based on characters of nest construction and breeding. Chapin (1917) did not mention *Passer* and its close allies in his important paper on the classification of the weaver-birds.

The major shift in thinking on the position of the passerine finches came with the publication of a series of papers by Sushkin (1924, 1925, 1927). On the basis of the structure of the horny palate, molt pattern and nest construction, he argued that the passerine finches should be removed from the Fringillidae and placed in the Ploceidae. Further, he stated that the genus *Montifringilla* of the "Catalogue of Birds in the British Museum" is an artificial taxon and should be split into *Montifringilla (nivalis)* and seven other species as recognized by Peters) which is allied to *Passer*, and *Leucosticte* (the rosy finches, *arctoa* and two other species as recognized by Peters) which is a true cardueline finch. The passerine finches, comprising the currently recognized genera *Passer*, *Montifringilla* and *Petronia*, were placed in a distinct subfamily, the Passerinae. Sushkin (1927, Fig. 16 and p. 28) believed the Passerinae to be an advanced group within the Ploceidae and to have evolved from the Plocepasserinae. Sushkin's conclusions were accepted immediately and have been followed by most subsequent workers. Nevertheless, a careful reading of his three papers revealed that Sushkin's conclusions were supported by little factual evidence and that this factual material was not presented and discussed in a systematic fashion.

Beecher (1953) and Tordoff (1954) concurred with Sushkin in placing the Passerinae in the Ploceidae. Beecher included the Viduinae and the Passerinae as advanced members of the Ploceidae and he separated this family from the Estrildidae. Moreover he separates these two families widely from the Fringillidae. Tordoff included the cardueline finches with the weaver finches (ploceids plus estrildids) which partly obscures his conclusions on the position of *Passer*. Few workers agreed with Tordoff's treatment of the carduelines (e. g., Mayr, Andrew and Hinde, 1956; Ziswiler,

1965). More interesting is Tordoff's (1954: 22) suggestion that the African genus *Poliospiza* (e.g. *leucopygia*) should be placed in the Passerinae. Currently, this genus is included in *Serinus* of the Carduelinae (Peters' Check-list XIV: 208), but no one has checked Tordoff's suggestion using additional anatomical material¹⁾.

The most important recent studies on the relationships of the nine-primaried finches and of the weaver finches are those by Ziswiler (1965, 1967 a, 1967 b, 1967 c, 1968) and his students (Ackermann, 1967, and Foelix, 1970) based on the structure of the horny palate, method of seed-husking and many details of the morphology of the alimentary canal. He showed that a sharp morphological distinction exists between the characters of the nine-primaried finches (e.g. the Fringillidae s.l., which includes the Carduelinae) and those of the Ploceidae and the Estrildidae. And he concluded that these groups of finches are not closely related within the oscines which should be reflected in the classification of the order. Moreover, Ziswiler (1967 a) placed the ploceid and estrildid finches in distinct families which he regards not to be closely related to one another. The Passerinae are included in the Ploceidae s.s., as a subfamily. But Ziswiler also included those plocepasserine genera, *Plocepasser*, *Pseudonigrita* and *Philetairus*, he studied in the Passerinae; these genera had been placed by Sushkin and several workers in the Plocepasserinae, a group distinct from and believed to be ancestral to the Passerinae. Further, Ziswiler (1968) regarded the genus *Sporopipes* as a distinct, specialized member of the Ploceidae that should be placed in a monotypic subfamily, the Sporopipinae.

Ziswiler (1965) followed Beecher (1954), Steiner (1960) and Nicolai (1964) in placing the Viduinae in the Ploceidae, stating that they originated from a stock close to the genus *Euplectes*. However, Friedmann (1960, 1962) argued that the Viduinae should be placed in the Estrildidae or closely allied to that group.

(One should note that problems exist in the nomenclature of these groups depending on whether an author regards the Ploceidae and the Estrildidae as distinct families or as subfamilies of the same family, the Ploceidae in the broadest sense. Not all of the subfamilies of the Ploceidae s.s. become tribes or other lower groups within the Ploceinae s.l. if the estrildids are included in the Ploceidae; some groups are sufficiently distinct that they would remain subfamilies of an enlarged Ploceidae. These nomenclatural problems must be kept in mind when reading the literature to avoid misunderstanding the conclusions of the author.)

Collias and Collias (1964, 1977) retained *Passer* in the Ploceidae, but stated that the nest of this genus does not show the weaving character-

¹⁾ In the meantime it has been shown that Tordoff's suggestions were based on the examination of a misidentified skeleton of *Vidua* sp. (R. L. Zusi, 1978, Bull. Brit. Orn. Cl. 98: 8). — W.

istic of the Ploceinae or even the close regular thatching of grass-stems characteristic of the Ploceipasserinae.

Sibley (1970) on the basis of egg-white proteins and Bulatova (1973) on the basis of karyotypes differ from the general consensus of opinion on the affinities of these birds. Bulatova (1973: 238) concluded that the karyotypes of *Passer* differ strongly from those of other Ploceinae s.l. and from those of the Estrildinae. Moreover, she concluded that the karyotypes of *Pyrgilauda* (= *Montifringilla*), *Montifringilla* and *Petronia* are much closer to those of finches (= Fringillidae) than to those of *Passer*. These conclusions are difficult to evaluate because much of the comparative data of karyotypes of the fringillid and ploceid finches used by Bulatova is scattered in the Russian and the Japanese literature. Sibley concluded that *Passer* is unlike the Ploceidae in egg-white proteins, but may be close to the fringillid finches. Further, he doubted that *Montifringilla* is closely related to *Passer* and concluded that it should be retained in the Ploceidae. More interesting are his conclusions that the egg-white pattern of *Vidua* is like that of *Passer* and unlike that of the ploceids, and that *Philetairus* may be closer to *Passer* than to the ploceid in its egg-white structure. Thus, both authors agree that *Passer* differs from the other passerine finches, but disagree sharply on the affinities of *Passer* and of the remaining passerine genera to the fringillid finches and to the ploceid finches.

The arrangement of the Ploceidae followed in Peters' "Check-list" (vol. XV, 1962) groups the plocepasserine genera, including *Sporopipes* and the passerine genera together in the subfamily Passerinae following the Bubalornithinae.

A brief mention should be made of *Petronia brachydactyla* (Peters; vol. XV, p. 23). This species was included by Sharpe in *Petronia* and retained there by Sushkin when he argued that the passerine finches should be removed from the Fringillidae to the Ploceidae. No mention was made by Sushkin on whether he examined anatomical material of this species. Recent observations by Professor H. Mendelssohn and his students at the University of Tel Aviv (pers. comm.) on the breeding behavior of *brachydactyla* convinced them that this species is erroneously included in *Petronia*. They conclude that this bird is a cardueline finch and should be placed in the monotypic genus *Carpospiza*. Unfortunately we were unable to examine any anatomical specimens on this species and cannot comment further on their conclusions which we accept. Comments on the morphology and affinities of *Petronia* do not apply to *brachydactyla* pending the publication of Professor Mendelssohn's findings.

Certainly the conclusions that can be reached about the monophyly of the passerine finches and about their relationships to other finches on the

basis of the evidence present in the above cited papers are inconclusive at best. Indeed, with the exception of the series of papers by Ziswiler and his students, most of the presented evidence is inconclusive. It should be noted that the question of the affinities of the passerine finches was peripheral to the central goal of most of these papers. The evidence amassed by Ziswiler provides a far stronger argument for separating the passerine finches from the Fringillidae than for including them in the Ploceidae, although none of his comparative observations are in conflict with the hypothesis that the Passerinae are members of the Ploceidae. Nest construction remains one of the major pieces of evidence supporting the relationships of the passerines to the weaver finches.

Taxonomic expressions for the relationships of the passerine finches have ranged, in recent years, from placing them in a separate family, the Passeridae which are usually placed next to the Ploceidae, to including them in the Ploceidae as a subfamily. Some workers include the ploce-passerine genera in the Passerinae while others exclude them. No recent worker formally included the passerine finches in the Fringillidae or in the New World nine-primaried oscines even if they had suggested that one or more of these genera may be allied to these groups.

The preglossale

The preglossale (Figs. 1, 2) is a small skeletal element articulating with the anterior tips of the paired paraglossalia of the tongue skeleton; details of its morphology are given in Bock and Morony (1978).

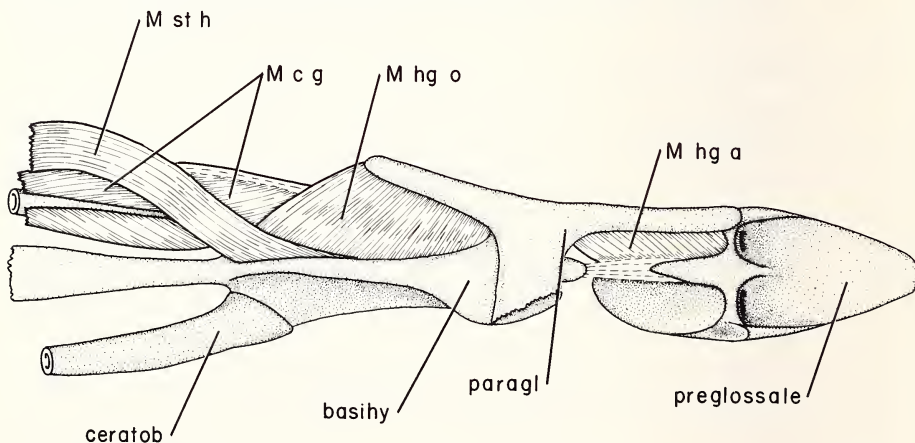


Fig. 1: Dorsal view of the tongue skeleto-muscular system of *Passer* to show the relationship of the preglossale to the rest of the tongue apparatus. The seed-cup has been removed as have the muscles and the paraglossale from the right side. The transverse and posterior longitudinal septa, the resulting anterior and two posterior (one still containing the *M. hg. anterior*) chambers and the ligamentous connection with the basihyal of the preglossale can all be seen. See text for abbreviations.

Morphology: In structure, the preglossale is an elongated, dorsally open trough or bowl (Fig. 1) that is broadly triangular in lateral view (Fig. 2). Its dorsal concavity is divided into three chambers — a single anterior one and a pair of posterior ones — by a transverse septum and a posterior longitudinal septum; the transverse septum lies at the midpoint of the preglossale, level with its paraglossal articulations. The preglossale is a partly ossified endochondral bone. It articulates with the paraglossalia by a pair of diarthroses and is connected to the basihyale by a stout ligament. The paired hypoglossus anterior muscles originate from the two posterior chambers of the preglossale and insert onto the ventromedial surface of the anterior body of each paraglossale. The anterior chamber of the preglossale contains the thick epidermal pad that comprises the seed-cup (Fig. 2). Numerous dermal papillae project into the epidermal pad; these are arranged in a regular pattern of about 15—20 rows each containing 6—8 papillae. Touch sensory corpuscles lie in the dorsal end of each papilla just below the surface of the seed-cup.

Function: It is not possible to speak meaningfully of the function of the preglossale as an isolated feature because this bone is part of a functional complex including the anterior end of the paraglossalia, the paired Mm. hypoglossus anterior and the seed-cup. At the minimum, one must consider the skeletomuscular system of the preglossale and M. hypoglossus anterior. As such, the preglossal complex functions to support the seed-cup and to modify its shape. The first is achieved by the presence of the preglossale under the base of the heavy epidermal pad of the seed-cup. The second is achieved by the whole preglossal skeletomuscular complex. Contraction of the M. hg. anterior rotates the preglossale around its paraglossal articulations, thereby depressing the anterior end of the preglossale. The result would be a downward bending of the anterior part of the seed-cup with its dorsal surface becoming more convex. The significances of this modification of the seed-cup — whether it permits better seed orientation or increases the sensitivity of the sensory corpuscles — for seed-husking and of its possible role in the feeding habits of the passerine finches are not known.

The seed-cup in the passerine finches, as in all finches, serves to orient the seed and hold it in place between the jaws during husking. Ziswiler (1965) has presented an excellent analysis of seed-husking in the major groups and of the morphological adaptations associated with seed-husking. The seed-cup of the tongue is a thick unkeratinized epidermal pad that helps support the seed. The slightly yielding nature of the epidermal pad conforms to the shape of the seed and permits distribution of force to the tongue without damage to any of the tissues.

The regular pattern of dermal papillae with the contained touch sensory organs provides a battery of sensory inputs by which the bird can detect

the position of the seed on the seed-cup and hence in the mouth. Ziswiler and his students (pers. comm.) in Zürich are currently studying the morphology of the sensory organs associated with the seed-cup in the several major groups of finches.

Comparison: A survey of the tip of the tongue in various groups of finches was undertaken to compare the bone-muscle system of this region and its relationship to the seed-cup. We are especially interested in the presence or absence of the preglossale, the presence or absence of the *M. hypoglossus* anterior, the structure of the *M. genioglossus* and the structure of the paraglossale. We wished to sample a diversity of genera from all groups of finches; time and material did not permit examination of all genera. We did, however, make a special effort to obtain all genera of passerine and plocepasserine finches. Our classification follows that used in Peters' "Check-list" except that we separate the plocepasserines from the passerines.

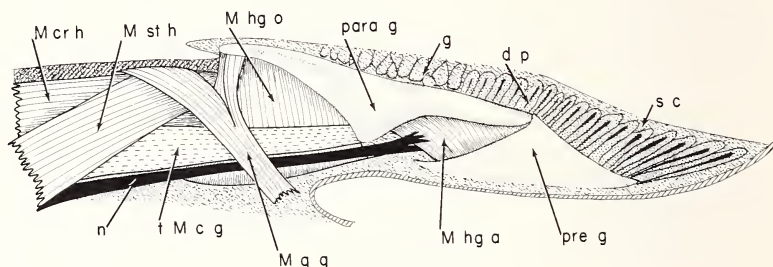


Fig. 2: The tongue of *Passer* seen in lateral view to show the skeletomuscular system against the background of the corneous tongue, including the seed-cup. The relationship of the preglossale to the seed-cup and to the paraglossale can be seen. Note that contraction of the *M. hg. anterior* would rotate the anterior end of the preglossale downward and thereby deform the seed-cup.

The illustrations were drawn directly from preparations of the tongue. These were prepared by dissecting the tongue from the head and removing the hyoid horns. A midsagittal cut with a sharp scalpel was made through the epidermis and dermis of the tongue, but not into the muscles and bones. The overlying epidermis, dermis and connective tissue were dissected away from the right side of the tongue to leave the muscle-bone system against the outline of the corneous tongue, including the seed-cup. The preparation was pinned to a wax-bottom dish so that an exact lateral view could be drawn.

Passeridae: Specimens of *Passer*, *Montifringilla* and *Petronia* were examined. Unfortunately, only a skeleton of *Petronia* was available, but the preglossale was still attached to the rest of the tongue skeleton.

Morphology of the tongue of *Montifringilla* was identical in all important aspects to that of *Passer* (Fig. 2). The preglossale of *Passer* articulates with the paraglossale. A portion of the M. hg. anterior can be seen between the two bones. The thick seed-cup with its dermal papillae and sensory corpuscles lies dorsal to the preglossale. Mucous salivary glands lie dorsal to the paraglossale and posterior to the seed-cup. Note that the anterior tip of the paraglossale ends well dorsal in the corneous tongue; it does not terminate close to the ventral surface of the tongue. The M. genio-glossus which originates from the mandibular symphysis, divides into two slips just before its insertion onto the posterior end of the paraglossale and into the mucosa dorsal to the other jaw muscle in the area slightly anterior to the glottis.

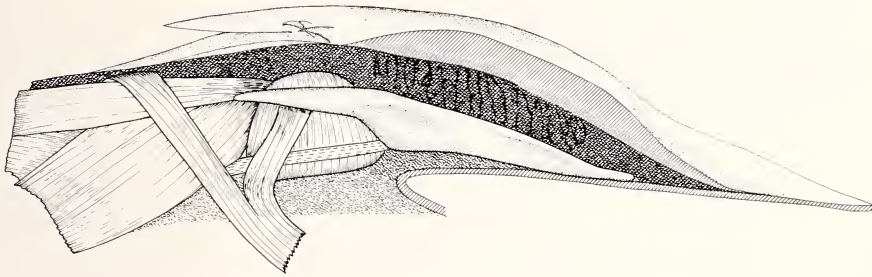


Fig. 3: The tongue of *Dinemellia* seen in lateral view.

Ploceidae; Bubalornithinae: We were able to examine both *Bubalornis* and *Dinemellia* which are similar in the morphology of their tongue; the following description is based on *Dinemellia* (Fig. 3). The paraglossale is large with a bulbous anterior body that extends to the ventral surface of the tongue; the two paraglossalia meet at their anterior ends. A thick epidermal pad of the seed-cup overlies the paraglossalia. It was not possible to determine with certainty the arrangement of dermal papillae and sensory organs in the epidermal pad in most of these preparations as we worked on the gross morphological level. We will not consider this aspect of the tongue morphology, but defer to the work of Ziswiler and his students (in litt). The M. hg. anterior is absent and no sign of a preglossale exists. The M. genio-glossus divides into two slips that insert onto the posterior tip of the paraglossale and into the dorsal mucosa.

Plocepasserinae: We were able to examine all genera of plocepasserine finches recognized in Peters, namely *Plocepasser*, *Histurgops*, *Pseudonigrita* (Fig. 4), *Philetairus* and *Sporopipes* (Fig. 5). Their morphology was quite similar and much like that in the Bubalornithinae. The paraglossalia are slender and longer with their anterior tips terminating close to the

ventral surface of the tongue. The seed-cup is rather thin. The M. hg. anterior and the preglossale are absent. The M. genioglossus divides and inserts onto the paraglossale and into the dorsal mucosa as in the Bubalornithinae.

Ploceinae: We dissected only the genera *Amblyospiza*, *Ploceus* (Fig. 6), *Euplectes* and *Foudia* in this subfamily. Much of the tongue morphology is similar to that found in the plocepasserine genera. The paraglossalia are long, slender and terminate at the ventral surface of the tongue, the

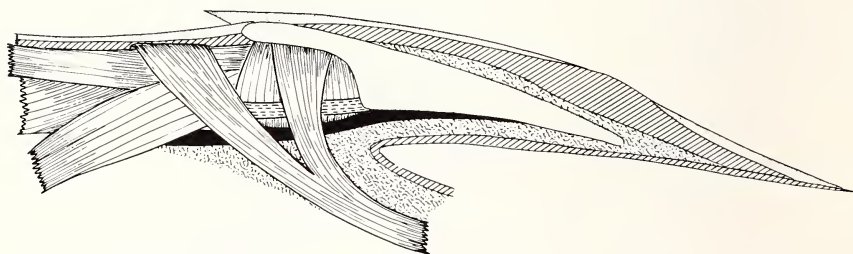


Fig. 4: The tongue of *Pseudonigrita* seen in lateral view.

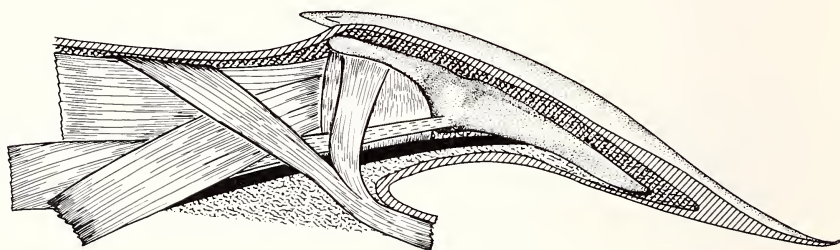


Fig. 5: The tongue of *Sporopipes* seen in lateral view.

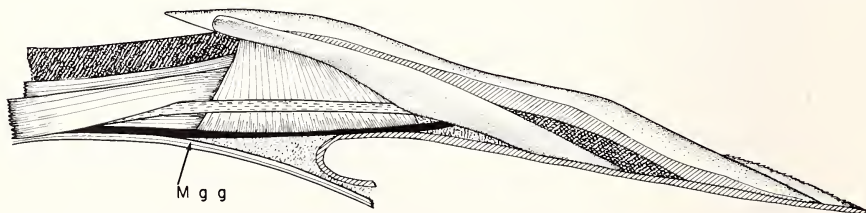


Fig. 6: The tongue of *Ploceus* seen in lateral view.

seed-cup is thin, and the preglossale and M. hg. anterior are absent. Most notable is the insertion of the M. genioglossus in *Ploceus* which inserts (noted by an asterisk) into the ventral mucosa of the tongue superficial to the M. stylohyoideus (Fig. 7). The musculature must be dissected with care to separate the insertion of the M. genioglossus from the body of the M. stylohyoideus; these muscles are not continuous, i. e., their fibers are not connected nor do they merge. In *Foudia* most of the fibers

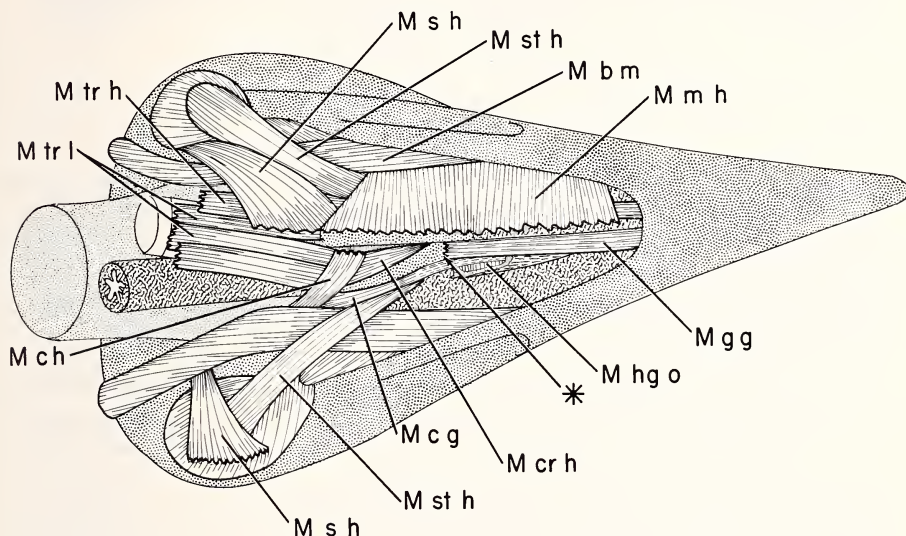
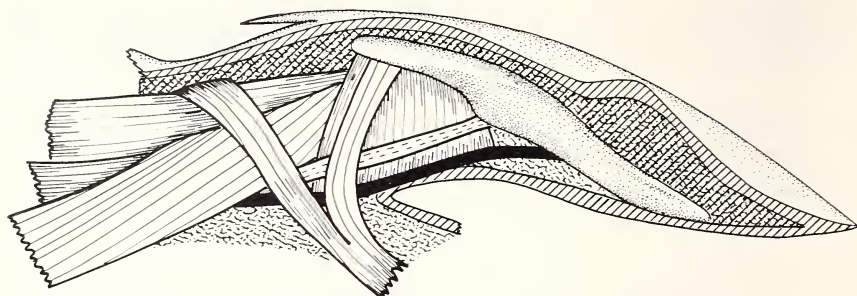


Fig. 7: The tongue musculature of *Ploceus* seen in ventral view to show the insertion (marked with an asterisk) of the M. genioglossus (M gg) into the mucosa of the ventral edge of the tongue. Because the mucosa has been dissected away with the rest of the overlying tissue, the muscle appears to end abruptly without attaching to any structure. It is not continuous with the M. ceratoglossus (M c g) or any other tongue muscle.

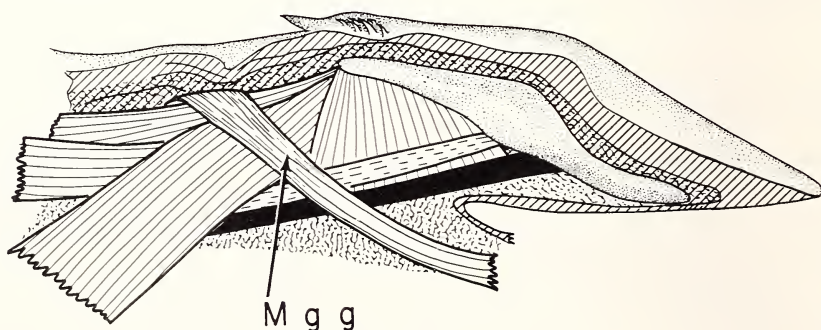
of the M. genioglossus insert ventrally but some curve dorsally and insert into the dorsal mucosa similar to the posterior slip of this muscle in the plocepasserines and most other passerine birds. This condition of the M. genioglossus is not seen in any other passerine bird, and we cannot provide any functional explanation for its evolution from the normal passeriform arrangement.

Viduinae: We examined the tongue of *Vidua* (Fig. 8) which is much like that of the other ploceids except for a shorter, thicker seed-cup. The paraglossale is broadly sigmoid in shape and terminates at the ventral edge of the tongue. The preglossale and M. hg. anterior are absent. And

Fig. 8: The tongue of *Vidua* seen in lateral view.

the two insertions of the M. genioglossus are onto the paraglossale and into the dorsal mucosa as normal for passeriform birds. It should be noted, although we do not wish to draw any conclusions at this time, that the morphology of the tongue (those parts examined in this study) in *Vidua* is similar to those of the Plocepasserinae or the Estrildidae, not to that of the Ploceinae.

Estrildidae: Of the many genera in this family, we examined only *Estrilda* (Fig. 9), *Poephila*, *Lonchura* (Fig. 10) and *Amadina*; these were all similar to one another. The seed-cup is short and thick with a short and strongly sigmoid paraglossale that terminates at the ventral surface of the tongue. The preglossale and M. hg. anterior are absent. In *Lonchura*, the M. genioglossus divides into two slips and inserts on the paraglossale and into the dorsal mucosa. In *Estrilda* only the posterior slip inserting into the dorsal mucosa remains. Little or no taxonomic significance should be given to this difference.

Fig. 9: The tongue of *Estrilda* seen in lateral view.

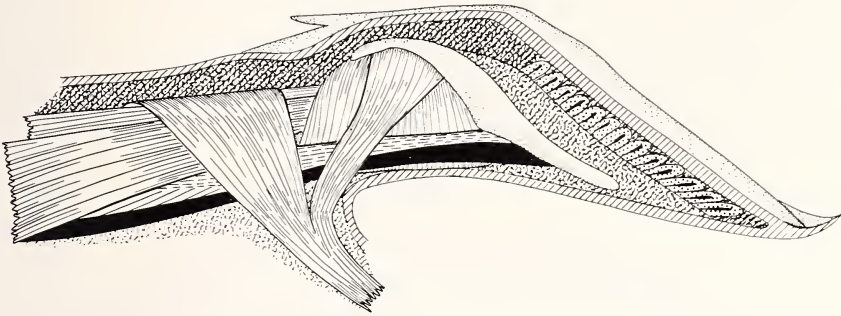


Fig. 10: The tongue of *Lonchura* seen in lateral view.

Fringillidae: We dissected *Fringilla* (Fig. 11), as a representative of the Fringillinae, and *Coccothraustes* ("Hesperiphona", Fig. 12), as a representative of the Carduelinae. The tongue of *Fringilla* is clearly less specialized than that of *Coccothraustes*. In *Fringilla*, the seed-cup is longer and not as thick as in *Coccothraustes*. Correspondingly, the paraglossale of *Fringilla* is more elongated and straighter while that of *Coccothraustes* is shorter and curved ventrally. The preglossale and the M. hg. anterior are absent in both. Both slips of insertion of the M. genioglossus exist in *Fringilla* while only the posterior one is found in *Coccothraustes*.

Emberizidae; Emberizinae: We dissected only *Spizella* (Fig. 13) to have a representative of the buntings; this group had never been considered to be closely related to the passerine finches. The seed-cup is thick and elongated with a corresponding lengthening of the paraglossale. The anterior end of this bone terminates close to the ventral surface of the tongue. No preglossale or M. hg. anterior exists in *Spizella*. And the M. genioglossus has the two usual slips of insertion.

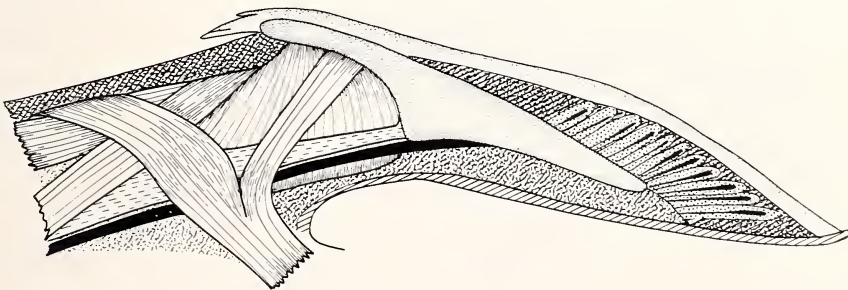


Fig. 11: The tongue of *Fringilla* seen in lateral view.

Cardinalinae: Again we examined only one genus, *Cardinalis* (Fig. 14), of this group because they had never been considered to be closely allied to the Passerinae. The seed-cup is relatively shorter and thicker than that of *Spizella* with the paraglossale slightly decurved to terminate at the ventral edge of the tongue. No preglossale or M. hg. anterior exist and the M. genioglossus has the two usual slips of insertion.

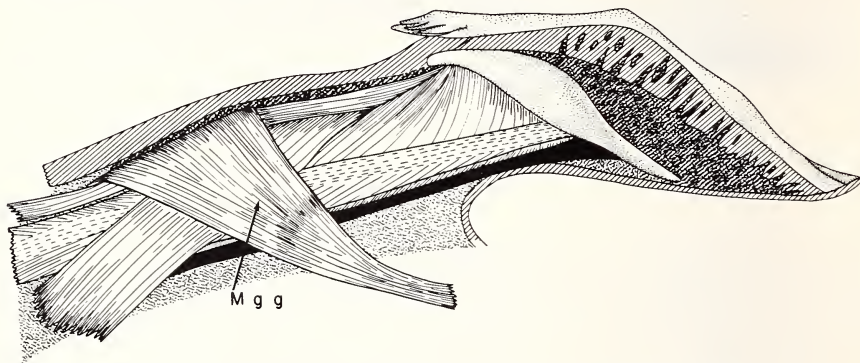


Fig. 12: The tongue of *Coccythraustes* seen in lateral view.

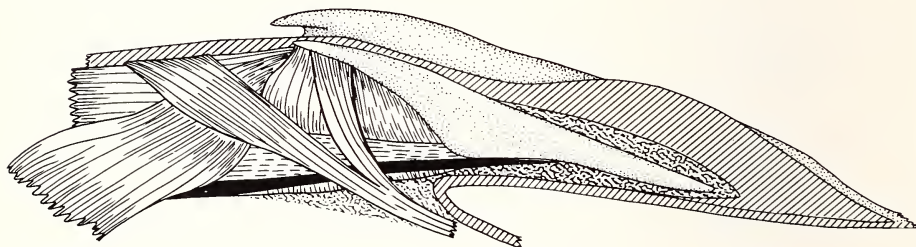


Fig. 13: The tongue of *Spizella* seen in lateral view.

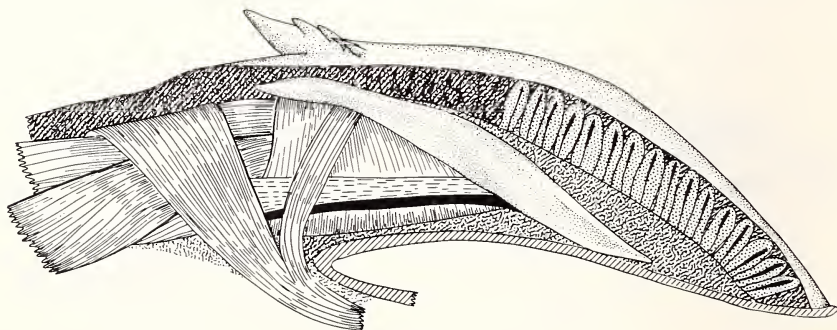


Fig. 14: The tongue of *Cardinalis* seen in lateral view.

Evolution: An essential step in testing character hypotheses about any feature is analysis of its plausible evolutionary history (Bock, 1977: 880—891, 892—893). This analysis usually depends on a complex argument woven from general theory and principles, special hypotheses and factual evidence. Often it may be necessary to include structures quite distinct from the feature under consideration. Central to the argument may be an understanding of how various types of structures, e. g. skeletal muscles or articulations, or how complex structural systems, e. g. bone-muscle, originate and evolve. Consideration of the evolution of particular structural complexes, such as vertebrate cranial kinesis, may be necessary. Feasible and nonfeasible patterns and directions of evolutionary change as well as constraints on the appearance and subsequent evolutionary modification of features are all important for full comprehension of the evolutionary history of a taxonomic character. Attention must be given to the use of causal relationships and sequence of arguments used in the testing of the diverse types of character hypotheses, e. g. establishment of transformation series, judgment of plesiomorphous-apomorphous relationships. This testing may depend far more upon establishment of correct series of arguments and secondary hypotheses than upon the number of final empirical observations. Comprehension of evolutionary mechanisms is central to the development of these argument chains.

Herein we will consider the conditions necessary for the evolutionary origin and further specialization of the preglossale, what restraints may exist, the evolution of associated features, e. g. the M. hypoglossus anterior, and so forth. The preglossale cannot be considered as an isolated feature when discussing its evolution, but must be treated, together with the M. hypoglossus anterior and the paraglossale, as part of a bone-muscle complex. And this complex must be viewed as an element within the seed-cup of the tongue which is a subunit of the feeding apparatus. A. holistic approach provides the firmest foundation for the evaluation of the evolutionary history of any individual feature.

Although the preglossale is an integral part of the seed-cup in the passerine finches, it is not an essential component of this structure as shown by the lack of the preglossale in all other finches. The detailed structure of the seed-cup in the varied groups of finches may be correlated with the mechanisms of seed-husking and with the amount and arrangement of the contained sensory corpuscles (Ziswiler, 1965, in litt.). The preglossale serves as support for the thick epidermal pad of the seed-cup. Further, the complex of the preglossale and the hypoglossus anterior muscle serves to bend the anterior part of the seed-cup ventrally and thereby deforms its dorsal surface into a more convex shape. Although the significance of this deformation is unknown, it is clear that the ability of the preglossale

to rotate about the tips of the paraglossalia is an essential aspect of its evolutionary history.

We conclude that the origin and specialization of the preglossale has been as part of a movable system; it is not just a static support of the seed-cup. If the latter were the case, then skeletal support of the seed-cup most probably would have fused solidly to the anterior bodies of the paraglossalia early in its evolution and would appear as a broad anterior plate connecting the tips of these bones. Quite likely, it might not have been recognized as a new feature unless detailed embryological studies were conducted (see below). Once the preglossale was fused to the tips of the paraglossalia, little cause would exist for the appearance or enlargement of the M. hg. anterior. This muscle must be present as a necessary prerequisite for the evolution of articulations between the preglossale and the paraglossalia.

As a movable support for the seed-cup, the origin of the preglossale was dependent upon the prior existence of the M. hypoglossus anterior. Presumably the preglossale originated as a heterotopic ossification lying along the origin of the paired Mm. hg. anterior. The primitive rod-like preglossale served to transfer the force of the muscle to the entire length of the seed-cup as well as supporting the latter structure; hence, the early preglossale must be viewed as a mechanical lever but without any direct attachment to the rest of the tongue skeleton. As this muscle increased in size and as its function of deforming the seed-cup (if this suggestion is correct) became more important, the need developed for a stronger compression strut between the origin and insertion of the M. hg. anterior. Proper functioning of any muscular system is dependent on the existence of an antagonistic force to every muscle and on the presence of an anticompression strut between the attachments of every muscle. This strut was provided by enlargement of the preglossale which grew until it abutted against the tips of the paraglossalia. Articulations evolved at this stage. Further enlargement of the preglossale to support the whole seed-cup would result in the dorsally opened-trough seen in the passerine finches.

The presence of well-developed diarthroses between the preglossale and paraglossalia supports, but does not prove, the conclusion that the preglossale evolved as a movable bone relative to the existing tongue skeleton. Articulations atrophy and the bones fuse during the life of an individual organism if the bones do not move relative to one another (Murray and Drachman, 1969). Yet, it is possible for articulations to develop within the limits of an embryonic bone if the bone is subjected to repeated bending as must have happened with the evolution of a true diarthrosis at the nasal-frontal hinge and/or at the anterior end of the jugal bar in

the skulls of parrots and some finches. Thus it is possible, but unlikely, that the paraglossal articulations of the preglossale evolved after the appearance of this bone as a fused anterior extension of the paraglossalia.

Most important is the presence of the M. hg. anterior as an essential prerequisite for the evolutionary origin of a movable preglossale as found in the passerine finches. Presence of articulations means that the bone moves and movement means that a muscle is present. The evolutionary history of this muscle in the passerine birds is thus of central importance. Our discussion is based on the comparative studies of the passerine tongue musculature by Bock and his associates (Bock, in litt.).

The M. hypoglossus anterior appears to be present in the passerine birds as an ancestral feature inherited from their nonpasserine ancestors. The M. hg. anterior is present in a broad diversity of groups within the Passeriformes that are not necessarily closely related to one another within the order. This muscle originates from a midventral raphe between the anterior bodies of the paraglossalia and inserts onto the medioventral surface of the paraglossale just anterior to its basihyale articulation. Usually the insertion is close to or continuous with the insertion of the M. ceratoglossus. Each M. hg. anterior is a unipinnate muscle; the pair of muscles forms a single bipinnate unit. Often it is a strong muscle for its mass as it contains many very short fibers. In a few groups, part of the M. hg. anterior inserts on the anterior tip of the basihyale. The M. hg. anterior varies greatly in size from a large muscle filling the space between the anterior bodies of the paraglossalia to a minute vestigial muscle that is difficult to find even with the aid of a dissecting microscope. In *Passer*, it is very large (Bock and Morony, 1978). Moreover, only in the passerine finches does the M. hg. anterior originate from a bony element instead of a fibrous raphe.

The M. hg. anterior is absent in a number of genera and families of passeriform birds; presumably it has been lost in the evolution of these groups. Thus, evolution of this muscle has been from the ancestral condition to varying size, to different attachments (e.g. insertion on the basihyale, and origin from the preglossale) and to total loss. Most important is that once it is lost, the M. hg. anterior or a similar muscle in the same position never reappears because there is no other muscle in this area from which a new "M. hg. anterior" could evolve. The evolutionary appearance of a new skeletal muscle is by splitting off of the new muscle from an existing one. This mode of evolution provides the new muscle with the necessary neural connections and skeletal attachments from those of the old muscle. To be functional, it is essential for a muscle to have motor nerve connections, sensory nerves and their endings within the muscle, the

proper central neural connections, and attachments (resistance) to the skeleton or other structures of the body. If any of these components are absent, the muscle would not function. And functionless muscles (e. g., muscles which do not operate fully) do not exist. Such muscles would atrophy during the life of the individual organism even if they started to develop ontogenetically. This generalization is supported by numerous experiments and accidents which show that whenever a muscle is denervated or tenotomized (one of the attachments cut), the muscle will atrophy. Hence, new muscles cannot appear "de novo" because all of these neural and skeletal connections must be present simultaneously with the muscular tissue. Because no other muscle lies in the tongue anterior to the paraglossal-basihyal articulation, the evolutionary appearance of a new muscle convergent to the lost M. hg. anterior would be extremely unlikely. Thus we conclude that evolution of the M. hg. anterior can only be in the direction of presence to loss; once lost, it is never regained. Further, we conclude that in the evolutionary history of the Passeriformes, a group possessing the M. hg. anterior could not have evolved from an ancestral group lacking it.

Details of the evolution of the preglossale are difficult to provide because of the absence of any intermediate conditions. We suggest that it appeared with the early stages in the evolution of the passerine seed-cup and that it was always associated with the M. hg. anterior. The preglossale became the origin for the already present M. hg. anterior. At this stage, this muscle was probably much smaller and similar in appearance to that seen in most other passeriform birds possessing it. The rudimentary preglossale presumably strengthened the origin of the M. hg. anterior. Extension of the preglossale anteriorly would connect it with the developing seed-cup and permit control of the position and shape (curvature of its dorsal surface) of the seed-cup by the M. hg. anterior. With increased force development of this muscle, the size of the preglossale increased and more importantly it reached and abutted again the anterior tips of the paraglossalia. At this point articulations developed between these bones. Now the neomorphic bone could serve as a compression strut between the origin and insertion of the M. hg. anterior, allowing a further increase in size of the muscle and a shift in the position of its origin to a more ventral position.

Discussion

The factual findings and arguments presented above permit the following conclusions on the diverse character hypotheses about the preglossale and associated features and on the several classificatory and phylo-

genetic hypotheses about the passerine finches, presented in the introduction.

Character hypotheses: Five hypotheses were postulated in the introduction. Definite conclusions can be reached on each, as follows:

1) The preglossale is homologous in the three genera possessing it as a skeletal element lying anterior to and articulating with the paraglossalia, serving as the origin for the M. hg. anterior and supporting the seed-cup. This hypothesis is tested and supported by the similar morphology of the preglossale, including details of the transverse and longitudinal septa, in these birds. Further, the preglossale has similar connections with other features such as the origin of the M. hg. anterior from its posterior chambers, the ligamentous connection to the anterior tip of the basihyale, articulations with the anterior ends of the paraglossalia and support for the base of the epidermal pad of the seed-cup. Therefore, we conclude that a preglossale was present in the ancestor of the three genera of passerine finches with a morphology similar to that seen in the living forms.

2) The preglossale is an apomorph (= derived feature) with respect to the ancestral condition of its absence in all other passerine birds, and indeed in all other birds. The preglossale lies anterior to the rest of the tongue skeleton which is part of the phylogenetically old hyoid gill arch of vertebrates. The bones of the tongue skeleton, as do all bones of the vertebrate gill arch series, develop ontogenetically from ectomesenchyme which arises from neural crest cells (Hörstadius, 1950). An excellent test of the apomorphous nature of the preglossale is to examine its ontogenetic development and ascertain whether it arises from ectomesenchyme or from endomesoderm. Such observations are not available. However, the available studies of the ontogeny of the tongue in *Passer* (Kallius, 1905; Saayman, 1963) show that the preglossale first appears late in ontogeny, just before hatching and long after the appearance of all other bones of the hyoid skeleton. These observations indicate that the preglossale has a different embryological development from that of the hyoid skeleton, and hence is not of ectomenchymal (= neural crest) origin. On this basis we conclude that the preglossale is an evolutionary neomorph or an apomorph compared to its absence.

It is more difficult to show that the lack of the preglossale is plesiomorphous in all groups. It is possible for the preglossale and M. hg. anterior to disappear completely leaving a tongue with a seed-cup, but lacking this complex. We doubt this possibility because the preglossale appears to be an integral part of the seed-cup in the passerine finches and we cannot comprehend a selection force that would favor the disappearance

of the preglossal complex in a finch. But we cannot offer any observations to test our conclusion. More difficult to judge are the changes in the tongue of a possible nonseed-eating descendent of the passerine finches. If the passerine finches had an insectivorous descendent that lost the seed-cup, then it is reasonable to expect a complete loss of the paraglossale with or without loss of the M. hg. anterior. We know of no way to distinguish between such a secondary loss of the preglossale — a further apomorphous stage relative to the presence of the preglossale — from the original absence of this feature.

3) The preglossale is a synapomorph (= homologous apomorph) in the genera of passerine finches; actually it is an autapomorph of this group. This conclusion is simply a conjunction of the previous two conclusions. We must emphasize that our conclusion that the preglossale is a synapomorph in the passerine finches is not because it is a shared derived feature in these birds, but because we have tested critically the hypothesis that the preglossale is homologous as an anterior tongue bone in these genera as well as the hypothesis that it is an apomorph with respect to its plesiomorphous absence. We have eliminated, as a real possibility, convergent evolution of the preglossale.

Further we would conclude that the taxonomic value of the preglossale is very great not because it is a synapomorph in the passerine birds, but because it is a new feature of complex structure and possessing a complex series of morphological connections with surrounding feature. We would conclude that the possibility of the preglossale evolving independently two or more times in the passerine finches is vanishingly low. In particular, we would argue for a greater taxonomic value of the preglossale compared to those shared apomorphs representing evolutionary loss of a structure or those about which nothing is known about their function or their possible evolutionary history.

4) On the basis of our discussion on the modes of evolutionary origin of a new muscle we conclude that the presence of the M. hg. anterior in passeriform birds is plesiomorphous and its absence is apomorphous. Once lost, this muscle is not regained. Shared loss of the M. hg. anterior is of little taxonomic value because of the great difficulty in separating synapomorphous loss with convergent loss.

5) We would accept the hypothesis that the enlarged M. hg. anterior with its sharply oblique fibers is homologous and apomorphous in the passerine finches compared with this muscle in other passeriform birds. The similar morphology of this muscle in passerine finches supports its homologous nature, but we cannot provide strong arguments supporting our conclusion of apomorphy and hence of synapomorphy.

Phylogenetic hypothesis about groups: Only one such hypothesis was put forth, namely that the passerine finches had to evolve from an ancestral group possessing the M. hg. anterior. We accept this hypothesis which is tested by the character hypothesis (# 4) that the lack of this muscle is apomorphous.

Classificatory hypotheses about groups: Several such hypotheses were postulated. These are concerned with the reality of the passerine finches as a taxon and the relationships of this taxon to other groups.

1) We accept the hypothesis that the passerine finches, the genera *Passer*, *Montifringilla* and *Petronia*, comprise a monophyletic and extremely closely knit group based on the structure of the tongue (synapomorphy of the preglossale, # 3, and of the passerine M. hg. anterior, # 5) and the evidence presented earlier by Sushkin, Ziswiler and other workers. This conclusion most likely does not hold for *Carpospiza* [*Petronia*] *brachydactyla*, pending publication of their findings by Mendelssohn and his associates (in litt.), which they believe to be a cardueline finch.

2) The evidence argues very strongly against the hypothesis that the passerine finches are members of the Fringillidae in the broad sense or in the sense of Peters' Check-list (vol. XIV, 1968). This follows from the group phylogenetic hypothesis presented above as all fringillid finches lack the M. hg. anterior. Moreover, the passerine finches could not be members of any group of advanced New World nine-primaried oscines because the M. hg. anterior was lost early in the evolution of the group.

3) In like fashion the evidence argues strongly against the hypothesis that the passerine finches are advanced members of the Ploceidae as concluded by Sushkin (1927: 28—29) and accepted by most workers because all members of the Ploceidae lack the M. hg. anterior.

4) The Passerinae of Peters' Check-list (vol. XV, 1962) are an artificial taxon and must be divided into at least two groups, the passerine genera and the rest. Several taxonomic solutions are possible. The most reasonable one is to reestablish the subfamily Plocepasserinae for the genera *Plocepasser*, *Histurgops*, *Pseudonigrita*, *Philetaurus* and *Sporopipes*. Another solution would be to unite the Plocepasserinae with the Bubalornithinae. Attention should be given to Ziswiler's (1968) conclusion that *Sporopipes* be placed in a monotypic subfamily which is in close agreement with Sushkin's (1927: 29) conclusion on the position of this genus.

5) The evidence is consistent with the hypothesis that the passerine finches are primitive members of the Ploceidae or of the New World nine-primaried oscines (Fig. 15). A little evidence (e.g., loss of the tenth primary, some aspects of skull morphology) supports the latter suggestion

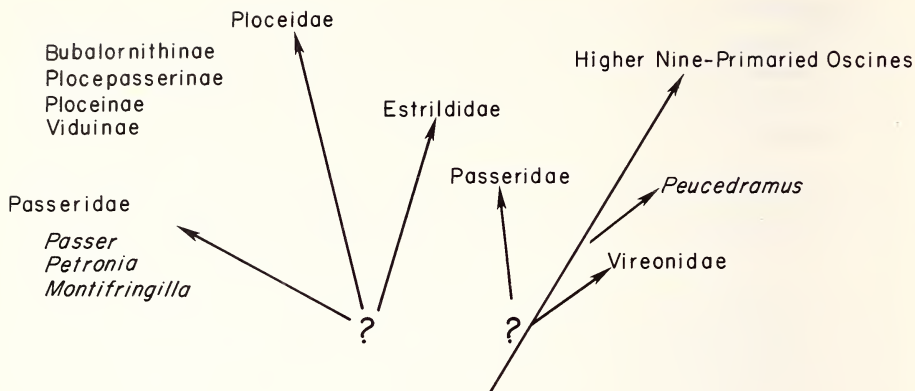


Fig. 15: Two schemes showing alternative ideas on the relationships of the passerine finches. The Passeridae may be an early offshoot of the Ploceidae-Estrildidae group or an early offshoot of the New World nine-primaried oscines. Although the evidence supporting either alternative is weak, more favors the first than any other available suggestion on the relationships of the passerine finches.

which can be set aside, but not rejected, for now. More evidence (e. g., Sushkin, 1927; Ziswiler, 1965; Collias and Collias, 1964) supports the former idea, but we do not believe that the available evidence is very convincing.

If the passerine finches are primitive members of the ploceid radiation, then we would argue that these birds acquired their seed-eating adaptations independently of the main complex of ploceid finches. The whole structure of the seed-cup in the passerine finches is different from that of the ploceid finches. The main feature uniting the passerines with the ploceids would be nest construction. Collias and Collias (1964) argue that the weaving abilities of *Passer* are very primitive compared to all ploceids which supports the hypothesis that the passerine finches are primitive members of the Ploceidae (see Ziswiler 1965: 42; Foelix, 1970: 584). But nest construction provides weak support on which to include the passerines in the Ploceidae. It would appear that the passerine finches are no closer to the Ploceidae than the latter are to the Estrildidae. If the argument of Ziswiler (1967 a: 509), that the Estrildidae show, at best, basal relationships to the Ploceidae but that these groups are distinct taxonomic families, is accepted as most workers do, then it seems reasonable to treat the passerine finches as a distinct family. This conclusion would be based on the contention that each of these groups, ploceids, estrildids, and passerids, acquired their seed-eating specializations independently. The alternative solution would be to place all of these groups in a broad Ploceidae with three subfamilies.

6) Thus, we accept the last of the classificatory hypotheses about groups proposed in the introduction that the passerine finches be treated as a distinct family — the Passeridae — and urge further intensive study to ascertain their affinities to other oscines, be it with the primitive New World nine-primaried oscines, the ploceid-estrildid complex, or some other group.

Summary

1) The preglossale is an evolutionary neomorph providing new evidence on the monophyly and relationships of the passerine finches. Analysis of this feature also provides a good example of proper methods of phylogenetic analysis.

2) The passerine finches could have only evolved from an ancestor possessing a *M. hypoglossus* anterior which excludes the Ploceidae, the Fringillidae and all other higher New World nine-primaried oscines.

3) The passerine finches, *Passer*, *Montifringilla* and *Petronia*, are a monophyletic group that should be classified as a distinct family, the Passeridae.

Zusammenfassung

1) Das Praeglossale der Sperlinge ist evolutionsgeschichtlich ein neomorphes Merkmal, das neues Licht auf die verwandtschaftlichen Beziehungen dieser Vögel zu werfen vermag. Die Analyse der hier vorliegenden Situation bietet auch ein gutes Beispiel für die einer phylogenetischen Auswertung angemessenen Methoden.

2) Die Sperlinge können nur von einem Vorfahr hergeleitet werden, der einen *M. hypoglossus* anterior besaß. Das schließt die Ploceidae, Fringillidae und alle höher entwickelten neunhandschwingigen Neuwelt-Oscines als Vorfahren aus.

3) Die Sperlinge, Gattungen *Passer*, *Montifringilla* und *Petronia*, bilden eine monophyletische Gruppe, die im System als eine besondere Familie, Passeridae, angesehen werden sollte.

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